

1 **How do intensive restoration efforts and climate changes**
2 **alter the strength of causal-feedback loops in Lake Taihu: A**
3 **tug-of-war**

4 Hui Fu^{1*}, Yili Ge¹, Guojun Cai¹, Jianmin Deng^{2*}, Huanyao Liu¹, Aiping Wu¹, Youzhi
5 Li¹, Wei Li³, Guixiang Yuan¹, Erik Jeppesen^{4,5,6,7,8}

6 ¹Ecology Department, College of Resources & Environments, Hunan Provincial Key
7 Laboratory of Rural Ecosystem Health in Dongting Lake Area, Hunan Agricultural
8 University, Changsha 410128, P. R. China

9 ²Taihu Laboratory for Lake Ecosystem Research, State Key Laboratory of Lake
10 Science and Environment, Nanjing Institute of Geography and Limnology, Chinese
11 Academy of Sciences, Nanjing, 210008, China

12 ³Research Institute of Ecology & Environmental Sciences, Nanchang Institute of
13 Technology, Nanchang 330099, P. R. China

14 ⁴Department of Bioscience and Centre for Water Technology (WATEC), Aarhus
15 University, Vejløvej 25, 8600 Silkeborg, Denmark

16 ⁵Sino-Danish Centre for Education and Research (SDC), University of Chinese
17 Academy of Sciences, Beijing, China

18 ⁶Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem
19 Research and Implementation, Middle East Technical University, Ankara, Turkey

20 ⁷Institute of Marine Sciences, Middle East Technical University, 33731 Erdemli-
21 Mersin, Turkey

22 ⁸Institute for Ecological Research and Pollution Control of Plateau Lakes, School of
23 Ecology and Environmental Science, Yunnan University, Kunming, China
24

25***Corresponding author.** Email: huifu367@163.com & jmdeng@niglas.ac.cn

26Abstract

27 Understanding how phytoplankton interacts with local and regional drivers as
28well as their feedbacks is a great challenge, and quantitative analyses of the regulating
29role of human activities and climate changes on these feedback loops are also limited.
30By using monthly monitoring dataset (2000-2017) from Lake Taihu and empirical
31dynamic modelling to construct causal networks, we quantified the strengths of causal
32feedbacks among phytoplankton, local environments, zooplankton, meteorology as
33well as global climate oscillation. Prevalent bidirectional causal linkages between
34phytoplankton and the tested drivers were found, providing holistic and quantitative
35evidence of the ubiquitous feedback loops. Phytoplankton exhibited the highest
36feedbacks with total inorganic nitrogen and ammonia and the lowest with nitrate. The
37feedbacks between phytoplankton and environmental factors from 2000 to 2017 could
38be classified by two groups: the local environments (e.g., nutrients, pH, transparency,
39zooplankton)-driven enhancement loops promoting the response of the phytoplankton,
40and the climate (e.g., wind speed)-driven regulatory loops suppressing it. The two
41counterbalance groups modified the emergent macroecological patterns. Our findings
42revealed that the causal feedback networks loosened significantly after 2007
43following nutrient loading reduction and unsuccessful biomanipulation restoration
44attempts by stocking carp. The strength of enhancement loops underwent marked
45decreases leading to reduced phytoplankton responses to the tested drivers, while the
46climate (decreasing wind speed, warming winter)-driven regulatory loops increased—
47like a tug-of-war. To counteract the self-amplifying feedback loops, the present

48eutrophication mitigation efforts, especially nutrient reduction, should be continued,
49and introduction of alternative measures to indirectly regulate the critical components
50(e.g., pH, Secchi depth, zooplankton biomass) of the loops would be beneficial.

51

52**Keywords:** Eutrophication, Feedback loops, Causal linkages, Convergent cross
53mapping, Lake ecosystem.

54Introduction

55 Lake eutrophication, which cause a shift from clear to turbid water in shallow
56lakes , has become a long-standing environmental challenge to water quality
57managers worldwide . This shift is largely attributed to an increase in external nutrient
58loading (e.g., nitrogen, N and phosphorus, P), breaking the macrophyte-dominated
59positive feedback loops in the clear water state and establishing phytoplankton
60dominated positive feedbacks . In the clear water state, macrophytes prevent sediment
61resuspension, oxidise the sediment, enhance water transparency, outcompete
62phytoplankton and eventually promote macrophyte growth , which lengthens and
63suppresses internal nutrient recycling . Phytoplankton-dominated feedbacks might
64form enhancement loops (e.g. elevated water pH and organic aggregates, reduced
65dissolved oxygen near the sediment and low water transparency, and stimulated P
66release from the sediment) that may lead to super linear relationships between
67phytoplankton and nutrients , while macrophyte-associated feedbacks working as
68important regulatory reducing phytoplankton proliferation (Moss, 1990; Søndergaard
69et al, 2017). Thus, there is growing evidence that the enhancement feedback loop
70would maintain and prolong the algae bloom), which, in turn, may delay the lake
71rehabilitation processes and counteract restoration efforts taken by the governments .

72 As any variations in the components (i.e., phytoplankton, nutrients, pH, SD,
73zooplankton) of the feedback loop might act as potential drivers enlarging or
74lessening its ecological consequences , external nutrient reduction is usually a
75practical and feasible way to combat eutrophication as well as nuisance blooms .

Likewise, the feedback loops may also be depressed by alternative eutrophication mitigation measures such as application of flocculants to decrease suspended particular and particular P as well as chemical inactivation agents to preserve P in sediments, and biomanipulation to control phytoplankton through a trophic cascade . However, as a coin has two sides, a series of potential drivers may push the feedback loop into a worse state by altering its components . For example, climate warming facilitates algae growth and aggravates the nuisance blooms , extreme rainfall brings nutrients (N, P) and suspended particulars (decreased SD) into lakes , and atmospheric stilling decreases non-algae turbidity and thus enhances the light availability for algae production . Therefore, to revert the feedback loops, lake managers may have to spend substantial investment for a long time period to combat deterioration .

Take Lake Taihu as an example. It is the third largest lake in China, and infamous for the water crisis in 2007 (Guo, 2007; Qin et al., 2010). Though a series of intensive restoration efforts have progressively been implemented since 2007 (Qin et al., 2019), the frequency and magnitude of algae blooms were not decreased as expected (Qin et al., 2021; Qin et al., 2019). For instance, in 2017, chlorophyll *a* (Chl) increased by nearly 80% but total phosphorus (TP) only by 31% compared to the average value across years (2005-2019) , suggesting super-linear (*slope* >1) relations (macroecological patterns) of logChl-logTP. This phenomenon might be attributed to a dominant self-amplifying feedback loops that regenerates nutrients to fuel algae. While the intensive restoration efforts might diminish the enhancement feedback loops or strengthen the regulatory feedback loops which could relieve cyanobacterial

98bloom (Qin et al., 2019; Schindler et al., 2016; Smith and Schindler, 2009), climate
99changes (e.g., warming, extreme rainfall, atmospheric stilling) might impede it (Yang
100et al., 2016; Zou et al., 2022), resembling a tug-of war (Guo et al., 2019; Meerhoff et
101al., 2022; Qin et al., 2021; Yan et al., 2017). So far, a holistic and quantitative
102assessment of the existence and strength of these self-reinforcing feedback loops as
103well as how they are modified by external drivers is unclear.

104 In this study, we assembled a long-term (2000-2017) dataset on Lake Taihu to
105construct the causal networks involving how phytoplankton interacted with water
106nutrients (i.e., nitrate, NO_3 , ammonium, NH_4 , total inorganic nitrogen, TIN and
107orthophosphate, PO_4), pH, SD and zooplankton. With the dataset we tested for the
108following hypothesised feedback loops (Fig. 1): nutrients \leftrightarrow Chl (i.e., chlorophyll a,
109used as a proxy of phytoplankton biomass) \leftrightarrow zooplankton \leftrightarrow nutrients; nutrients \leftrightarrow
110Chl \leftrightarrow pH/SD \leftrightarrow nutrients and referred it to the emerging macroecological patterns
111(EMPs, the estimated slope of the log-log linear relationships) of the phytoplankton
112response to bottom-up (e.g., TP, TN) and top-down (e.g., zooplankton) controls. We
113were also interested in exploring the causal linkages between the components of the
114local feedback loops and the regional and global drivers. Specifically, we addressed
115the following questions: (1) What is the relative importance of the distinct causal
116determinant for Chl? (2) which are the predominant local feedback loops associated
117with Chl and what is the potential influence of global climate oscillation and the
118regional meteorological forces on the components of feedback loops within the lake?
119(3) what is the relative importance of the enhancement and regulatory loops for

determining the EMPs of the phytoplankton response to bottom-up (e.g., TP, TN, SD) and top-down (e.g., zooplankton) controls? Last but not least, we assessed the temporal changes in the strength of these causal linkages across the studied periods and in how the intensive restoration efforts (IRE) implemented in Lake Taihu after 2007 alter their strength.

Materials and methods

Data collection

Lake Taihu, the third largest freshwater lake (2,338 km²) in China, is located in a highly developed region characterised by heavy urbanisation and industrialisation in the Yangtze River Delta. The lake has a mean depth of 1.9 m and a catchment area of about 36,500 km². It is fed by a number of tributaries (>200) that transport massive amounts of nutrients derived from the watershed into the lake, which is subjected to several rainfall events especially during summer (Yang et al., 2016). Eight sites (i.e., from Meiliang Bay to the centre of the lake, Fig. S1) have been monthly observed by the Taihu Laboratory for Lake Ecosystem Research (TLLER) since 1991, but more regularly since 2000. We compiled monthly observations of Chl (a proxy of phytoplankton biomass), TN, TP, PO₄, NO₃, NH₄ and TIN concentrations, pH, Secchi depth (SD) and zooplankton density (zoo) during the period 2000-2017 from the National Ecosystem Science Data Center (<http://www.nesdc.org.cn/>). Daily data on meteorological variables (2000-2017) at the Wuxi Meteorological Station near Lake Taihu, including air temperature (AirTemp), precipitation (Precip) and wind speed (WindSpeed), were collected from the China Meteorological Data Sharing

142Service System (<http://cdc.cma.gov.cn/>) and then calculated monthly average data for
143use in our analysis. The monthly anomalies (2000-2017) of El Niño and Southern
144Oscillation (ENSO), Pacific decadal oscillation (PDO) and the Atlantic multidecadal
145oscillation (AMO) were considered as a proxy of the global climatic oscillation, and
146oscillation information was obtained from the website of National Weather Service
147(<https://www.weather.gov/>).

148 We applied the monthly averaged data set (2000-2017) on all tested variables,
149yielding 1728 data records for local environmental variables across 8 sampling sites
150and 216 data records for the variables of the meteorological and global climatic
151oscillation (one data record for each month). The limited missing values ($< 5\%$) were
152interpolated using the “*na_seadec*” function in the R package of “*imputeTS*” . For
153each time series, the long-term linear trend was eliminated to ensure stationarity by
154using the residuals from a linear regression against time. As seasonality could have a
155confounding influence on the analysis, we deseasonalised the time series by scaling it
156against the mean and standard deviation of values occurring in the same month
157according to the equation: $(O(t_i) - \mu_i) / \sigma_i$, where μ_i is the monthly mean, and σ_i is the
158monthly standard deviation for the i (1, 2, ..., 12) month, and $O(t_i)$ is the original time
159series.

160 ***Strength of causal linkage and feedback loops***

161 We identified the causal linkages between pairs of time series (i.e., tested
162variables) using convergent cross mapping (CCM, see Supplementary methods),
163which is an empirical causality analysis based on Takens’ theorem for dynamical

164systems . We quantified the strength of causal linkages as the cross-mapping skill at
 165maximal library size, $\rho(L_{max})$, i.e. the greater the $\rho(L_{max})$, the stronger are the causal
 166effects. For instance, a strong causal effect of PO4 on Chl revealed by CCM indicated
 167that PO4 is a major driver for the dynamics of Chl (magnitude or variability). To
 168eliminate systematic differences (e.g., noise) in cross-mapping skill among the
 169sampling sites, the strength of causal linkages was standardised by dividing linkage
 170strength (LS) by the maximum within each site . The standardised linkage strength
 171(SLS) ranges from 0 to 1, where a value close to 1 indicates strong causal linkage and
 172vice versa with a value close to 0. We reconstructed causal networks (Fig. 1) and then
 173standardised the strength of causal linkages separately for each site as the distinct sites
 174might not have equivalent dynamics and belong to the same attractor.

175 The strength of pairwise and triple feedback loops was quantified using Neutel's
 176loop weight – the geometric mean of SLS for all linkages within a given feedback . In
 177a pairwise feedback ($X \leftrightarrow Y$), the loop weight is the geometric mean of the SLS in
 178both directions (i.e., $X \rightarrow Y$ and $Y \rightarrow X$). Likewise in a triple feedback, the loop
 179weight is the geometric mean of the SLS in a directed cyclic loop (i.e., Type I: $X \rightarrow Y$
 180 $\rightarrow Z \rightarrow X$; Type II: $X \rightarrow Z \rightarrow Y \rightarrow X$). To assess the linkage strength of the causal
 181pathway from global climate oscillation (e.g., ENSO, PDO, AMO) to the local
 182feedback loops via changes in meteorological variables, we calculated the geometric
 183mean of the SLS for all linkages in the pathway (i.e., $X \rightarrow Y \rightarrow Z$). To determine the
 184uncertainty of our estimates in causal strength and loop weight, we calculated their

185standard errors using the resampling method that reconstructed the sampling
186distributions from 500 random samples of embedded data points with replacement.

187***Enhancement and regulatory loops for emergent macroecological patterns***

188 We used a generalized least square (GLS) model with a temporal auto-
189regressive error structure (*corArma* function) to assess the log-linear relationships
190between Chl and TN, TP, SD and zooplankton biomass separately for each site. The
191slope estimated from the GLS model of Chl-TP, Chl-TN, Chl-SD relations and zoo-
192Chl relations was considered as emerging macroecological patterns of the response of
193phytoplankton to bottom-up ($EMP_{\text{bottom-up}}$: $EMP_{\text{Chl-TP}}$, $EMP_{\text{Chl-TN}}$, $EMP_{\text{Chl-SD}}$) and top-
194down ($EMP_{\text{top-down}}$: $EMP_{\text{zoo-Chl}}$) controls, respectively. The larger the values of EMP, the
195stronger the response of phytoplankton to the drivers and vice versa. We tested if there
196was a significant relationship between the EMP and the strength of causal linkages
197and feedback loops using *Spearman* correlation. The feedbacks that have positive
198relationships with EMP (positive values for $EMP_{\text{Chl-TP}}$, $EMP_{\text{Chl-TN}}$) and negative
199relationships (negative values for $EMP_{\text{Chl-SD}}$, $EMP_{\text{zoo-Chl}}$) could be considered as the
200enhancement loops of the EMP, promoting the phytoplankton response to the drivers,
201and *vice versa* for depressing the phytoplankton response to the drivers.

202 To further assess the relative importance of these feedbacks for determining the
203EMP, we used random forests regression (RF) – a bootstrapping classification tree .
204RF does not only avoid the issue of over-fit (i.e., there are many more responsible
205variables than for the 8 samples in our study), it also deals efficiently with the spatial
206autocorrelation among the samples . For each of the four EMPs, we built RF for the

207significant causal linkages and feedback loops according to the above *Spearman*
208correlation as potential predictors that were randomly resampled to generate 500 un-
209pruned decision trees. The relative importance of each variable was evaluated
210according to the increments in mean standard error (MSE) for the RF model
211predictions. In addition, to assess the relative contribution of enhancement loops and
212regulatory loops to each EMP, we calculated the percentages of the sum of MSE for
213all enhancement or regulatory loops dividing them by total MSE for all significant
214feedback loops with a positive value.

215 ***Temporal variations in the strength of causal linkages***

216 We estimated the temporal changes in causal linkages using two complementary
217approaches. First, we compared the overall strength of causal linkages and feedbacks
218among the tested variables between the two distinct periods according to the
219implementation of intensive restoration efforts (IRE) (Pre-IRE: 2000-2007; Post-IRE:
2202008-2017) by conducting the CCM analysis and measurements of SLS and loop
221weights separately for each period. Then, we used *permutation* test ($N = 9999$) to
222compare the strength of the two distinct causal linkages or feedback loops across time
223series (2000-2017) and to test if the same causal linkages or feedback loops differed
224between the two periods (i.e., Pre-IRE and Post-IRE).

225 Second, we quantified the time-varying (i.e., dynamic) interaction for each pair
226of causal linkage (e.g., $X \rightarrow Y$). With this, we applied the multivariate S-map method
227(i.e., a locally weighted multivariate linear regression, see Supplementary methods) to
228estimate the strength and direction of the interaction between ecological components

229by recovering the Jacobian elements at each time point . For each pair of causal
230linkage, we first calculated the dynamic interaction strength (DIS) as the mean value
231of S-map coefficients for each time step across 8 sampling sites and then used
232Kendall's τ test to assess the significance of temporal trends. The Kendall's τ test was
233conducted with several time series: 1) whole time series, 2) within seasonal time
234points (e.g., spring, summer, autumn, winter), 3) within distinct periods (e.g., Pre-
235IRE: 2000-2007; Post-IRE: 2008-2017).

236 All statistical tests were performed using R version 4.01 software (R Core Team.
2372018). CCM and multivariate S-map were performed using the *rEDM* package
238(<https://github.com/SugiharaLab/rEDM>) in R (v-0.7.5) . The basic ideas of CCM are
239described in brief animations: tinyurl.com/EDM-intro, and the detailed information to
240perform EDM analyses can be found at
241<https://deepeco.ucsd.edu/resources/#pagecontent>. We performed Kendall's τ test using
242the function *mann-kendall* in the R package.

243Results

244Causal linkages

245 Based on CCM analysis (Table S1), we found significant causal linkages with
246Chl for the local drivers (e.g., SD, pH, NO₃, PO₄, NH₄, TIN, zooplankton)as well as
247the regional drivers (e.g., AirTemp, Precip, WindSpeed). According to the permutation
248test for the SLS between the distinct causal linkages, we found that phytoplankton
249was most sensitive to NH₄ and TIN among the tested drivers (Fig. 2A, all $P < 0.05$)
250and showed a stronger response to PO₄ than to NO₃ (Fig. 2A, $P < 0.05$). Notably, the

average strength of the causal effects of local physico-chemical environments (e.g., SD, pH) and zooplankton on Chl was comparable with that of PO₄ (Fig. 2A, $P > 0.05$).

In the opposite direction, the SLS of Chl→PO₄ was significantly stronger than Chl→NO₃ (Fig. 2B, $P = 0.027$) but not significantly different from Chl→NH₄ and Chl→TIN (Fig. 2B, $P > 0.05$). The causal effects of phytoplankton on the other local drivers (i.e., SD, pH, zooplankton) were as strong as those on PO₄ (Fig. 2B, all $P > 0.05$). However, there was no significant difference between the two directions for the same pairs of variables (Fig. 2A & 2B, e.g., Chl→PO₄ vs. PO₄→Chl, all $P > 0.05$) except for a markedly higher NH₄→Chl than Chl→NH₄ (Fig. 2A & 2B, $P < 0.05$).

The causal effects of regional drivers on phytoplankton (e.g., AirTemp→Chl, Precip→Chl, WindSpeed→Chl) are shown in Fig. 2D, and their effect strengths were significantly lower than those of the local drivers (all $P < 0.05$). In addition, significant causal effects of global climate oscillation on regional meteorological variables were observed for PDO→WindSpeed, ENSO→AirTemp and ENSO→WindSpeed (Table S3 online), while the strength of their causal pathways to Chl via wind speed was usually stronger than via the other meteorological variables (Fig. 2D, all $P < 0.05$).

Feedback loops

We quantified the strength of all potential pairwise and triple feedback loops. For the pairwise feedback loops, we found the lowest strength for NO₃↔Chl (Fig. 2C, all $P < 0.05$) and the highest for NH₄↔Chl (Fig. 2C, all $P < 0.05$). Notably, the

other pairwise feedback loops between phytoplankton and physico-chemical environments (i.e., pH, SD) as well as predators (i.e., zooplankton) were as strong as $\text{PO}_4/\text{TIN}/\text{NH}_4 \leftrightarrow \text{Chl}$ (Fig. 2C, $P > 0.05$). Also, the strength of pairwise feedback loops between variables without Chl was assessed (Fig. S3); here $\text{TIN} \leftrightarrow \text{pH}$ and $\text{TIN} \leftrightarrow \text{zoo}$ had the highest average strength, followed by $\text{NH}_4 \leftrightarrow \text{zoo}$, $\text{NO}_3/\text{NH}_4 \leftrightarrow \text{pH}$. For the triple feedback loops, there were no significant in-between differences (Fig. 2E&2F, all $P > 0.05$), and the PO_4 -associated triple feedbacks were as strong as the N -associated triple feedbacks (i.e., NH_4 , NO_3 , TIN) ones (Fig. 2E&2F, all $P > 0.05$).

Enhancement and regulatory loops controlling emergent macroecological patterns

The causal linkages and feedbacks were ubiquitous in Lake Taihu and occurred either as enhancement or regulatory loops, contributing to the emergent macroecological patterns (EMPs) of the phytoplankton response to major drivers (Fig. S4), with 19 significant enhancement loops and 5 regulatory loops for $\text{EMP}_{\text{Chl-TP}}$ (Fig. S4A), 12 enhancement loops and 7 regulatory loops for $\text{EMP}_{\text{Chl-TN}}$ (Fig. S4B), 21 enhancement loops and 4 regulatory loops for $\text{EMP}_{\text{Chl-SD}}$ (Fig. S4C), 5 enhancement loops and 1 regulatory loop for $\text{EMP}_{\text{zoo-Chl}}$ (Fig. S4D).

Random forest analysis revealed that the enhancement loops for EMPs were mainly characterised as local environment- (e.g., nutrients, SD, pH and zooplankton) associated feedbacks, and the regulatory loops for EMPs were indicative of regional climate- (e.g., wind speed) associated feedbacks (Fig. 3). For these tested feedbacks, a remarkable higher importance of enhancement loops than of regulatory loops was detected in determining $\text{EMP}_{\text{Chl-TP}}$ (Fig. 3A), $\text{EMP}_{\text{Chl-SD}}$ (Fig. 3C) and $\text{EMP}_{\text{Chl-zoo}}$ (Fig.

2953D), while the importance of enhancement loops and regulatory loops in affecting
296EMP_{Chl-TN} was comparable (Fig. 3B).

297 *Temporal changes in the strength of causal linkages and feedbacks*

298 CCM analysis identified a significant decrease in the strength of 5 causal
299 linkages, 5 causal pathways, 4 pairwise feedbacks and 14 triple feedbacks (Fig. 4).
300 Among these, Windspeed→Chl and AMO→Windspeed→Chl were important
301 regulatory loops for EMP_{bottom-up}, TIN→Chl and TIN↔Chl were important
302 enhancement loops for EMP_{Chl-TP}, and EMP_{Chl-TN}, zoo↔Chl was an important
303 regulatory loop for EMP_{Chl-zoo}. For the triple feedback loops,
304 PO₄/NH₄/TIN→Chl→SD→PO₄/NH₄/TIN, NH₄/NO₃→Chl→zoo→NH₄ /NO₃
305 were important enhancement loops for EMP_{Chl-TP}, TIN→Chl→SD→TIN was an
306 important enhancement loop for EMP_{Chl-TP} and EMP_{Chl-SD}, PO₄→Chl→pH→PO₄,
307 NH₄/NO₃/TIN→Chl→zoo→NH₄ /NO₃/ TIN were important enhancement loops for
308 EMP_{Chl-SD}, SD→pH→Chl→SD was an important enhancement loop for EMP_{Chl-zoo}.

309 S-map analysis revealed that the interactions between the ecological factors are
310 dynamic (i.e., time-varying) rather than static (Fig. 4). We found a significant
311 temporal trend in the dynamic interaction strengths (DIS) of a series of causal
312 linkages (Fig. 4), with decreasing trends for Chl→NH₄/NO₃/PO₄ and NO₃→Chl and
313 increasing trends for Chl→TIN and Precip→Chl. In addition, we observed that DIS
314 differed among seasons (Fig. 6). In spring across the study period (2000-2017), DIS
315 decreased significantly for zoo→Chl. In summer, DIS increased significantly for
316 zoo→Chl and Chl→TIN, while it decreased for PO₄→Chl. In autumn, DIS increased

317significantly for zoo/TIN→Chl, and decreased for Chl→PO₄/NO₃/NH₄/SD/pH/ and
318PO₄/NO₃/SD→Chl. In winter, DIS increased significantly for
319NH₄/NO₃/AirTemp→Chl and Chl→PO₄/NO₃/NH₄/ pH and decreased for
320zoo/pH/TIN/Precip→Chl.

321Discussion

322 We used empirical dynamic modelling (e.g., CCM, S-map) to detect the causal
323effects and the feedback interactions among the ecological components in Lake Taihu
324during the last two decades. Our results quantified the casual feedback networks
325between phytoplankton, water nutrients, physical environments and zooplankton,
326meteorology as well as global climate oscillation, and quantify the strength of casual
327linkages and feedback loops. The feedbacks were distinguished into the enhancement
328and regulatory loops in determining the EMPs of phytoplankton's response to bottom-
329up and top-down controls, and their temporal changes were assessed.

330Causal effects of environmental factors on phytoplankton

331 We found a greater sensitivity of phytoplankton to NH₄ than to NO₃ which
332corresponds well with the fact that phytoplankton generally prefer NH₄ due to the
333lower energetic costs of uptake and assimilation . Previous findings from Lake Taihu
334also revealed that NH₄ was the most important predictor of total phytoplankton
335biomass and cyanobacteria . The lower causal effects of PO₄ than of NH₄ on Chl
336might reflect the lower variation in PO₄ (constantly high) in Lake Taihu.

337 The observed strong effects of zooplankton on Chl suggest that the temporal
338dynamics of the zooplankton community were encoded in that of phytoplankton, and

we clearly captured the cue of the top-down effects on the phytoplankton in the lake. Consistently, [Mao et al. \(2020\)](#) found that the phytoplankton biomass was positively associated with benthivorous and zooplanktivorous fish and negatively with zooplankton biomass, demonstrating that the trophic cascade effects, as fish and zooplankton (43.2%) were comparable with those nutrient effects (40.9%) in controlling the phytoplankton biomass in the lake. In addition, analyses of data from 233 Danish lakes, lab and full-scale field experiments highlighted the occurrence of top-down control by fish in shallow lakes. Considering the strong trophic cascade in Lake Taihu, the temporal dynamics of the fish community would be encoded in both the phytoplankton and the zooplankton, and direct and indirect (e.g., trophic cascade) causal effects of the fish community on phytoplankton (top-down forces) would be expected.

Our results elucidated that the local physico-chemical environments (e.g., pH, SD) overall affected Chl to the same extent as PO₄ (bottom-up) and zooplankton (top-down), implying that several previous studies on Lake Taihu (focusing on the role of nutrient effects only) might have underestimated the impact of physico-chemical forces on phytoplankton. Besides, the effect strengths of regional drivers (e.g., air temperature, precipitation, wind speed) were significantly lower than those of local drivers (all $P < 0.05$), which is consistent with previous findings from lab and field studies. Importantly, our results suggest that regional meteorological drivers mediated a cascading effect of the global climate changes on the phytoplankton, as found by other studies. Moreover, except for Chl, significant causal effects of meteorological

361variables on the other local variables were observed (Fig.S2), supporting the
362expectation that the drivers from regional to global scale would have a profound
363influence on the components of the feedback loops .

364*Feedbacks of phytoplankton on environmental factors*

365 Besides the causal effects of environmental drivers on phytoplankton, the
366comparable feedbacks, both of pairwise ones and triple ones were also documented.
367The feedbacks were highest for $\text{NH}_4 \leftrightarrow \text{Chl}$, as well as typical bottom-up (nutrients \rightarrow
368 $\text{Chl} \rightarrow$ zooplankton \rightarrow nutrients) vs. top-down (nutrients \rightarrow zooplankton \rightarrow $\text{Chl} \rightarrow$
369nutrients), physico-chemical drivers (nutrients \rightarrow $\text{Chl} \rightarrow$ pH/SD \rightarrow nutrients vs.
370nutrients \rightarrow pH/SD \rightarrow $\text{Chl} \rightarrow$ nutrients), characterised physico-chemical
371environment-mediated predator-prey cycles (pH/SD \rightarrow $\text{Chl} \rightarrow$ zooplankton \rightarrow pH/SD
372vs. pH/SD \rightarrow zooplankton \rightarrow $\text{Chl} \rightarrow$ pH/SD). This echo effect supports the idea that
373phytoplankton has important feedback impacts on the physico-chemical environment,
374the nutrient recycling, and as well as predators.

375 The prevalence of the bidirectional causal linkages between pairs of local
376variables (Fig. S1, Table S2), especially regarding phytoplankton biomass (Chl),
377provides robust evidence for the hypothesised feedback loops. Phytoplankton first
378decreases dissolved nutrient abundance by direct uptake, and then return inorganic
379nutrient back to the water after death; but the rate of nutrient recycling is difficult to
380measure, and may differ between N and P . The notable causal effects of
381phytoplankton accompanied with physico-chemical drivers (Fig. S2) on nutrients
382highlight the importance of water column nutrient recycling processes . Besides, the

383strong feedback strength between zooplankton and especially N (e.g., TIN, NH₄)
384(Fig. S2) emphasizes that the zooplankton community plays an important role in
385nutrient recycling and phytoplankton growth by excretion . Furthermore, the
386concurrent changes in the phytoplankton and thus zooplankton community (Özkan et
387al, 2014) may entail a highly coupled feedback loops that influence nutrients
388recycling and stoichiometry of the lake ecosystems.

389 The feedbacks of Chl to zooplankton (bottom-up) and pH/SD reinforce the
390comprehensive interactions and thus feedback loops between phytoplankton and the
391physico-chemical environment as well as zooplankton (Matsuzaki et al., 2018). In the
392last four decades, Lake Taihu has experienced major physico-chemical changes
393including a pronounced rise of pH to 9-10, which may affect both phytoplankton and
394zooplankton composition and biomass. Algae proliferation fueled by eutrophication
395could greatly elevate pH and reduce SD, accelerating internal nutrients recycling).
396Moreover, the water level has increased 8.7% increase (0.25 m) and the water
397transparency has decreased 40-60%, which has profound effects on algae blooms and
398macrophyte loss . Therefore, our results supports that local physico-chemical drivers
399(e.g., pH, SD, dissolved oxygen, ultraviolet light) as well as predators (i.e.,
400zooplankton) may play a critical mediating role in augmenting or lessening the effects
401of phytoplankton on the nutrient recycling . Our results emphasized that these highly
402interactive components within the constructed causal network create not only efficient
403nutrient cycling but also integrative responses to environmental fluctuations.

404 *Enhancement and regulatory loops for emergent macroecological patterns*

405 Causal feedbacks were common in the lake as either enhancement or regulatory
406 loops contributing to the emergent macroecological patterns (EMPs) of the response
407 of phytoplankton to major drivers. We found that both enhancement and regulatory
408 loops controlled EMPs despite their distinct relative importance. Furthermore, our
409 findings revealed that the algae biomass in the lake might be controlled by both local
410 environment-driven enhancement loops and climate-driven (here wind speed)
411 regulatory loops. This suggests that any variation in these local drivers will strengthen
412 (e.g., nutrient inputs, higher pH or turbidity) or weaken (e.g., nutrient reductions,
413 lower pH or increased water transparency) the enhancement loops, which intensified
414 the phytoplankton responses to the bottom-up and top-down controls. In this regard,
415 all loop components act as both “cause” and “effect” variables, and a holistic and
416 integrative view of managing lake ecosystems should be taken. It is noteworthy that
417 the widely used eutrophication mitigation measures in Lake Taihu have greatly
418 reduced the external nutrients input and altered the fish community composition ,
419 which (at least for nutrients) weakened the control by the enhancement loops of the
420 phytoplankton biomass, as indicated by our results(Fig. 3&4).

421 The temporal dynamics of the regional climate strengthen (e.g., increased wind
422 speed) or weaken (e.g., atmosphere stilling) the regulatory loops, thus altering the
423 phytoplankton responses to the tested drivers. Although other variables were not
424 detected as components of the regulatory loops, our results revealed that intrinsically
425 regulatory mechanisms combat the observed self-amplified cycles that sustain algae

426blooms. Moreover, the dominant role of enhancement loops in controlling EMPs
427(EMP_{Chl-TP} , EMP_{Chl-SD} , $EMP_{Chl-zoo}$) may contribute to the high sensitivity of
428phytoplankton to variations in TP, water transparency and zooplankton. However, the
429comparable importance of enhancement loops and regulatory loops in affecting
430 EMP_{Chl-TN} may explain the relatively lower sensitivity of phytoplankton to the major
431decreases in TN in the lake.

432 *Temporal changes in the strength of causal linkages and feedbacks*

433 We also quantified the temporal changes in the strength of causal linkages and
434feedbacks in two dimensions: the overall causal strength based on CCM analysis
435within the two distinct periods (Pre-IRE: 2000-2007; Post-IRE: 2008-2017) and the
436dynamic interaction strength (DIS) assessed by the S-map method across the specific
437time series. Since 2007, a series of intensive restoration efforts (IRE) have been made
438by the local governments to combat algae blooms and improve water quality . The
439CCM analysis identified a significant decrease in the strength of several causal
440feedbacks (Fig. S5, Fig. 6), of which some belong to the enhancement or regulatory
441loops for the EMPs.

442 Significantly weaker feedback between phytoplankton and zooplankton were
443also detected during Post-IRE, which seems reasonable according to long-term
444observations of trophic interactions in Lake Taihu. Since 2008, biomanipulation by
445stocking of silver carp and bighead carp to control large-sized phytoplankton (e.g.
446cyanobacteria) has been conducted, potentially allowing zooplankton to better control
447the nanophytoplankton . Thus, stronger causal feedback between phytoplankton and

448 zooplankton would be expected. However, recent findings have indicated that the
 449 stocking of phytoplanktivorous fish enhances phytoplankton and cyanobacteria
 450 growth and diminishes the zooplankton biomass, the size of cladocerans as well as the
 451 zooplankton:phytoplankton ratio, which eventually weakens the grazing pressure of
 452 zooplankton on phytoplankton through a trophic cascade. Notably, the S-map results
 453 demonstrated a strong seasonal pattern of DIS between zooplankton and
 454 phytoplankton with increasing trends during summer and autumn and decreasing
 455 trends during winter and spring, which might contribute to a significant seasonality of
 456 predator-prey interactions - an area that warrants further studies.

457 Remarkably, weakened triple feedback loops characterised all the tested local
 458 environments (e.g., nutrients, pH, SD, zooplankton), which is greatly associated with
 459 the local environment-driven enhancement loops for the EMPs. Therefore,
 460 fluctuations in these components will have cascading influences on the efficiency of
 461 the enhancement loops in controlling the EMPs even though some of the weakened
 462 causal feedbacks (e.g., PO₄/pH/SD-associated causal linkages and pairwise
 463 feedbacks) are not included as enhancement loops. Overall, this common reduction of
 464 the strength of multiple causal interactions and the trophic cascade may give IRE a
 465 critical role in mitigating the self-amplifying feedback loops supporting algae blooms.

466 We observed significant decreases in the causal strength (CCM results) of
 467 regulatory loops, mainly for climate-associated feedbacks (e.g., wind speed). For
 468 Lake Taihu, [Deng et al. \(2018\)](#) revealed that a climatically-modulated decline in wind
 469 speed strongly contributed to the variations of Chl, and this decline appears to be

more significant after 2007. In addition, lower wind speed seems to have reduced non-algal turbidity by nearly 40% and increased the abundance of buoyant cyanobacteria after 2005, providing a “light niche” for phytoplankton and significantly promoting Chl sensitivity to nutrients. Besides, the significant decrease in the strength of causal pathways (e.g., ENSO/PDO→Precip→Chl, AMO/PDO→AirTemp→Chl) might also weaken the strength of causal feedback loops through the causal chain from global climate changes to phytoplankton via alterations in precipitation and air temperature. Furthermore, DIS (S-map method) showed increasing trends for AirTemp→Chl during winter, which is consistent with a previous study identifying a significant association between increased temperature and the sensitivity of Chl to nutrients only in February. These findings indicate that an alternative mechanism of increased time-lag sensitivity of phytoplankton to nutrients may explain the increasing frequency and magnitude of algae blooms after warmer winters. Overall, the weakened climate (especially wind speed, warming winter)-driven regulatory loops entail increased sensitivity of phytoplankton to local drivers, which might greatly offset the weaker enhancement loops (external nutrient reduction) by alleviating the phytoplankton response to local drivers.

Conclusion

Our results provide a holistic and quantitative evidence for the hypothesised feedback loops and demonstrate how phytoplankton interacts with the tested drivers. The observed common feedback loops reveal that algae proliferation may have a profound impact on the nutrient recycling, the local physico-chemical environment

492and zooplankton, while variations in the components of the feedback loop have the
493potential to lessen or strengthen it. Importantly, we also identified strong cascading
494causal effects of the global climate change on phytoplankton via changes in regional
495meteorological drivers (i.e., precipitation and air temperature) that importantly control
496the dynamics of the feedback loops. Furthermore, our study quantified that the
497emergent macroecological patterns of the response of phytoplankton to top-down and
498bottom-up controls are regulated by two kinds of counterbalance feedback loops: the
499enhancement loop that strengthens the phytoplankton response and the regulatory
500loop that suppresses it. Our findings highlight that the constructed causal feedback
501networks in Lake Taihu loosened significantly after 2007 as a series of local
502environment-driven enhancement loops underwent a marked decrease in strength
503during Post-IRE (intense restoration efforts, 2008-2017), indicating that IRE has the
504potential to combat viscous feedback loops. Moreover, the varying causal effects of
505global and regional climate changes on the components of the feedback loops will
506inevitably cause deterioration (i.e., increased sensitivity of phytoplankton to local
507drivers). Overall, the current IREs initiated to slow down the enhancement loops that
508trigger over-proliferation of phytoplankton is largely offset by the climate (especially
509decreasing wind speed, warming winter) and carp stocking, and does thus not suffice
510to weaken the sensitivity of phytoplankton to the local environment. To counteract the
511self-amplifying feedback loops, therefore, the present eutrophication mitigation
512efforts, especially long-term nutrient reduction, should be continued and introduction
513of some alternative measures to indirectly regulate the critical components (e.g., pH,

SD, zooplankton) of the loops would also be beneficial.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

H.F. and G.Y. conceived the research idea. H.F. analyzed the data with help from H.Y., A.W., Y.L., W.L., G.Y. and E.J.. Y.G., G.C., and J.D. collected the data. H.F., J.D., G.Y. and E.J. wrote the manuscript with critical comments from co-authors.

Data availability statement

We confirm that this manuscript is not under consideration by another journal and has not been published elsewhere. The dataset are available online.

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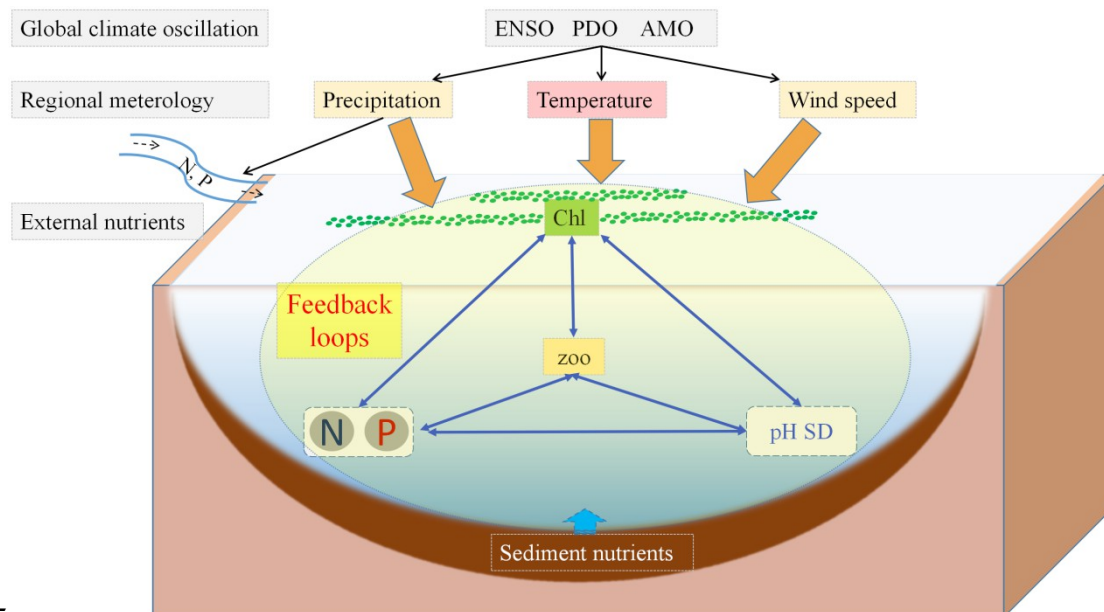
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705
706**Fig. 1** The hypothesized feedback loops between phytoplankton biomass (Chl) and
707local environments (N: nitrogen, P: phosphorus, pH, SD: Secchi depth), zooplankton
708(zoo), regional meteorology (precipitation, air temperature, wind speed), global
709climate oscillation (ENSO, PDO, AMO).
710

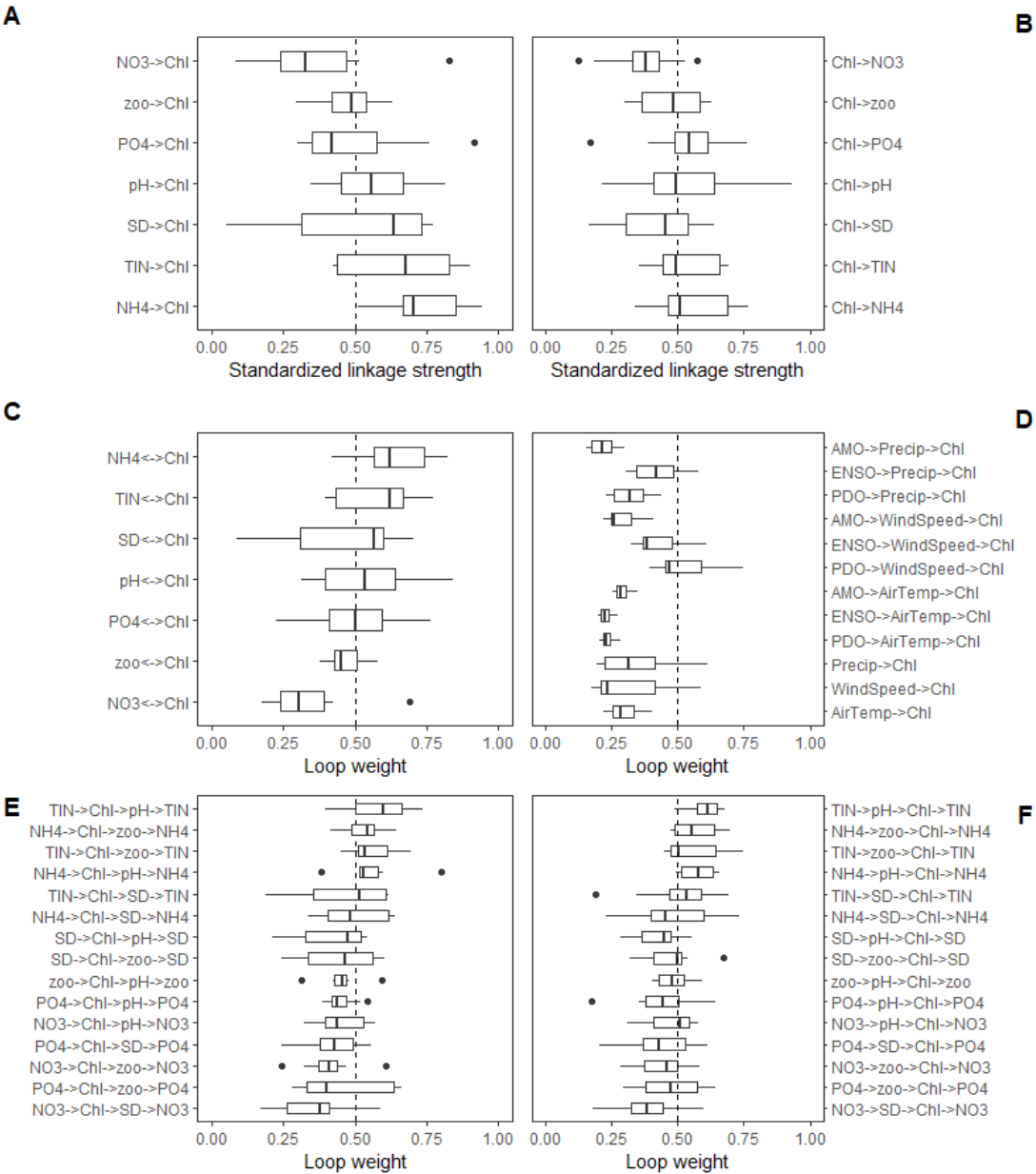


Fig. 2 Standardized linkage strength of casual linkages (A and B), loop weight of pairwise feedbacks (C), casual pathway (D) and triangle feedbacks (E and F) between the tested variables across the time series (2000-2017). Chl: chlorophyll a; NO3: nitrate; NH4: ammonium; TIN: total inorganic nitrogen; PO4: orthophosphate; SD: Secchi depth; zoo: zooplankton density.

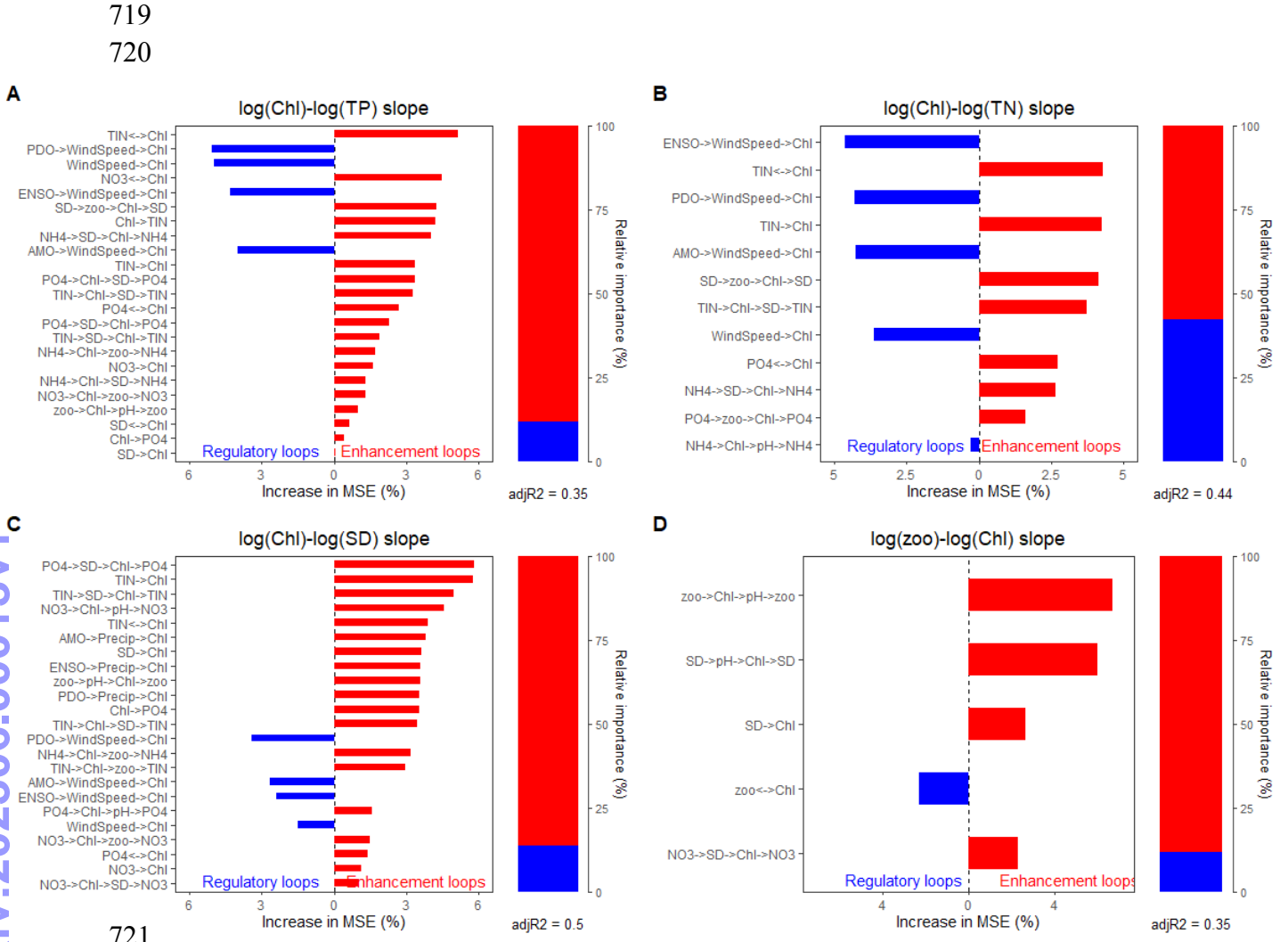
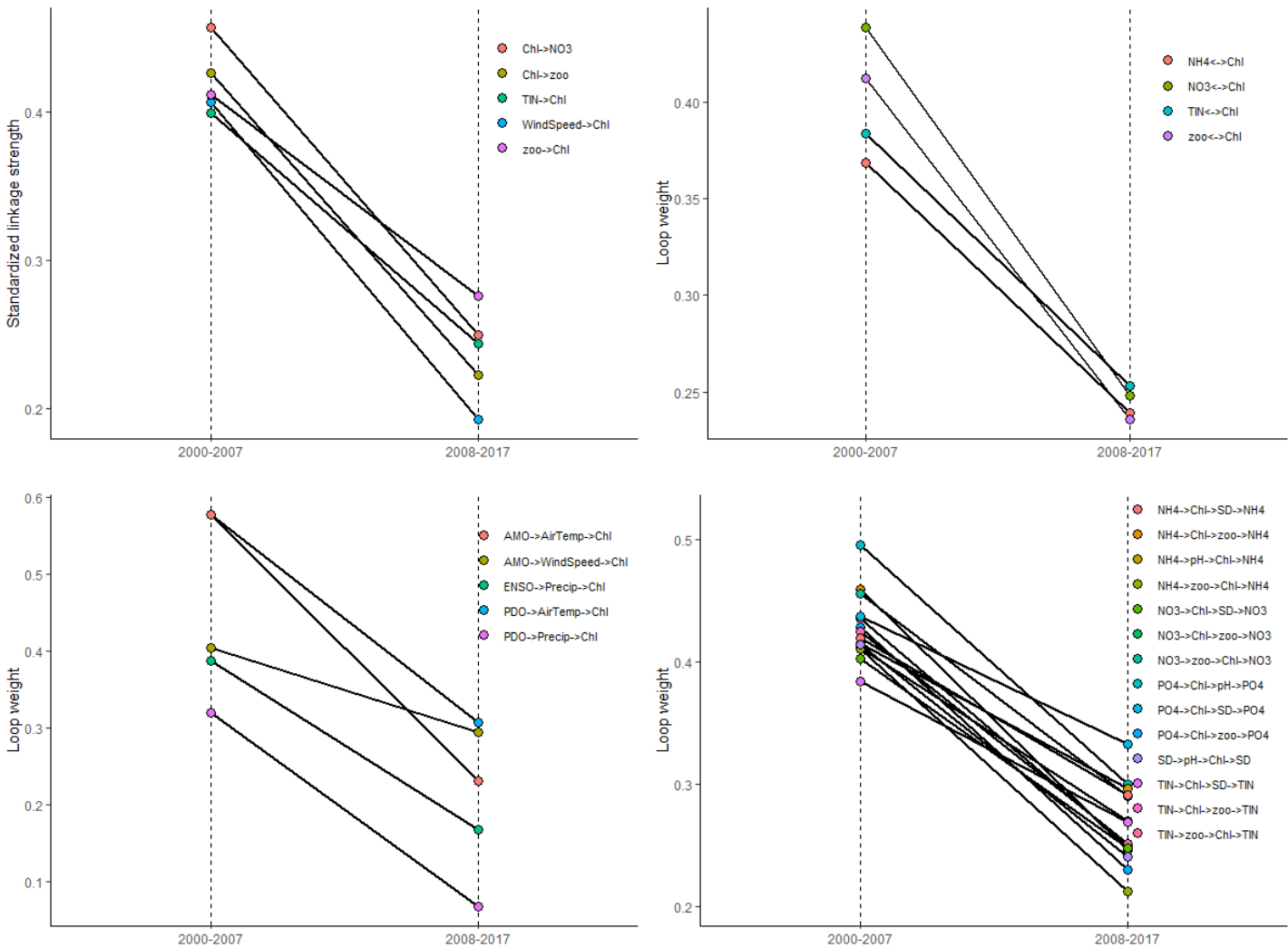


Fig. 3 Random forest reveals mean predictor importance (percentage of increase of mean square error, Increase in MSE) of each significant casual linkage and feedback in determining the emerging macroecological patterns (EMPs, the estimated slope of the log-log linear relationships) of the phytoplankton response to bottom-up (A: TP, B: TN, C: SD) and top-down (D: zooplankton) controls. The enhancement loops promote phytoplankton response to the drivers with positive relationships with positive EMPs (Chl-TP/TN) and negative relationships with negative EMPs (Chl-SD/zoo), while the regulatory loops depress phytoplankton response to the drivers. The relative contributions of pulled enhancement and regulatory loops were shown. Chl: chlorophyll a; NO3: nitrate; NH4: ammonium; TIN: total inorganic nitrogen; PO4: orthophosphate; SD: Secchi depth; zoo: zooplankton density.

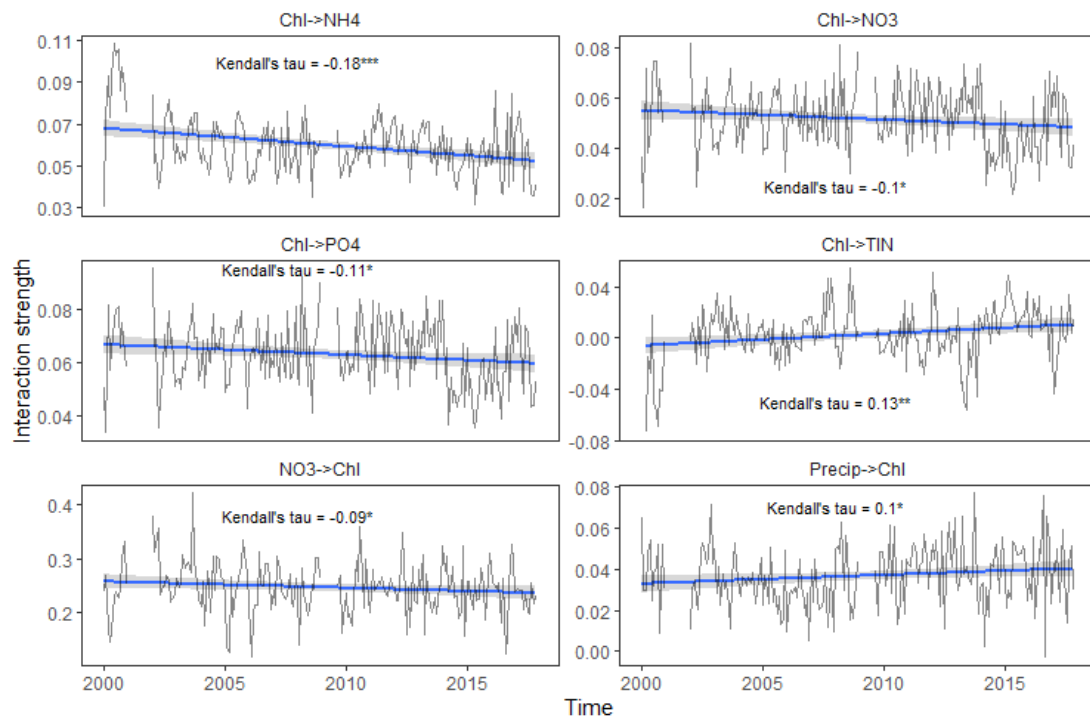
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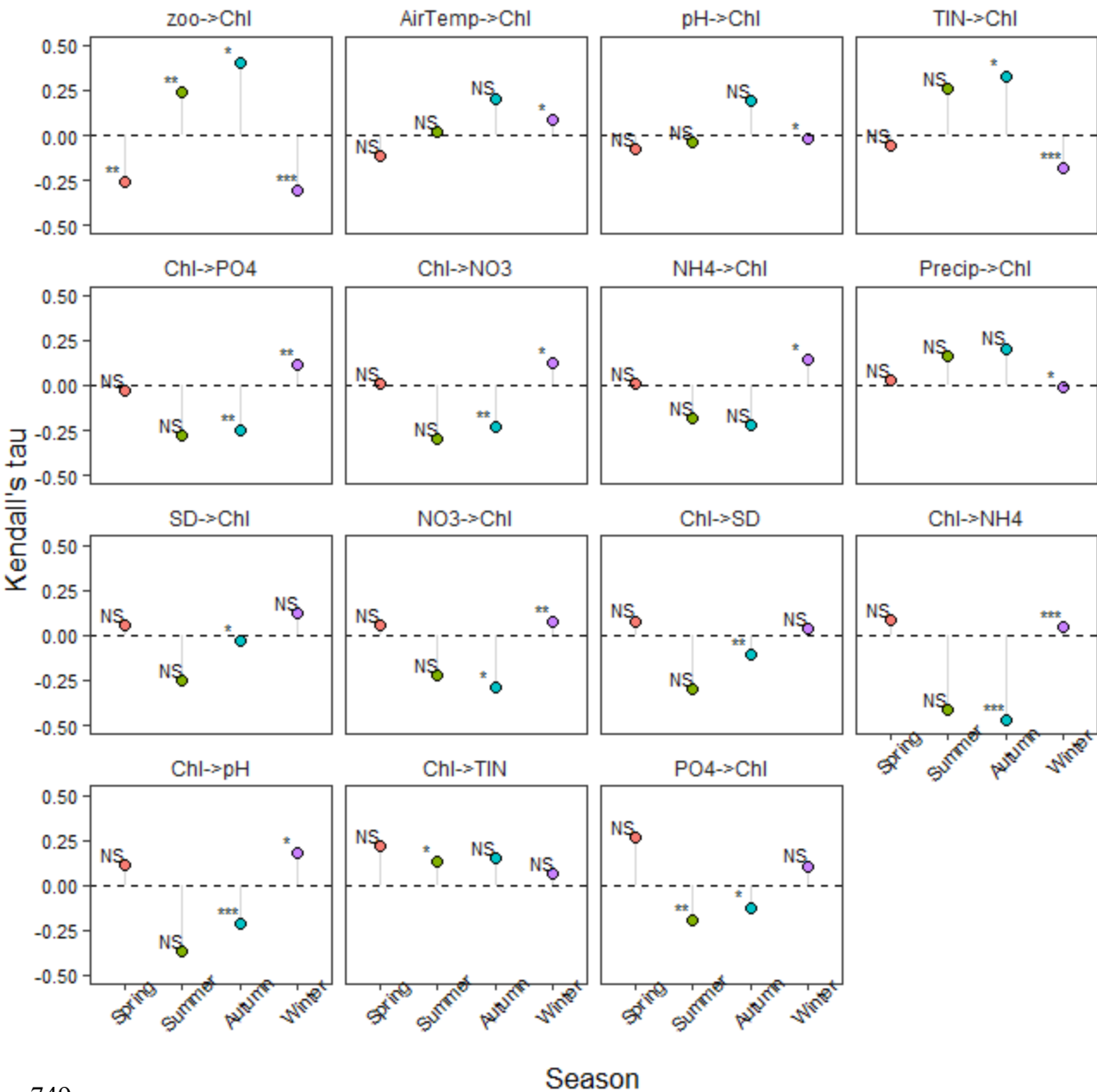
735**Fig. 4** Significant changes in the standardized linkage strength of causal linkages (A),
736loop weight of pairwise feedbacks (B) casual pathway (C) and triangle feedbacks (D)
737between the tested variables during two distinct periods (Pre-IRE: 2000-2007, Post-
738IRE: 2008-2017). Chl: chlorophyll a; NO3: nitrate; NH4: ammonium; TIN: total
739inorganic nitrogen; PO4: orthophosphate; SD: Secchi depth; zoo: zooplankton density.

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743**Fig. 5** Time-varying casual interactions with significant temporal trends across time
744series (monthly from 2000 to 2017) according to Kendall's τ test. Chl: chlorophyll a;
745NO3: nitrate; NH4: ammonium; PO4: orthophosphate; TIN: total inorganic nitrogen;
746Precip: precipitation. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

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750**Fig. 6** Results of Kendall's τ test for the time-varying casual interactions involving
751phytoplankton during four seasons. Chl: chlorophyll a; NO3: nitrate; NH4:
752ammonium; TIN: total inorganic nitrogen; PO4: orthophosphate; SD: Secchi depth;
753zoo: zooplankton density, AirTemp: air temperature; Precip: precipitation. *: $p < 0.05$,
754*: $p < 0.01$, ***: $p < 0.001$, NS: not significant.

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